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Diel variation in nectar production of *Bomarea costaricensis* (Amaryllidaceae)

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Abstract: Temporal and spatial patterns of nectar production may be adaptations to the foraging patterns of the hummingbirds that pollinate them. We hypothesized that *Bomarea costaricensis*, a hummingbird-pollinated plant of the tropical highlands of Cerro de la Muerte, Costa Rica, varies its diel pattern of nectar production in relation to the foraging schedule of hummingbirds. We predicted that nectar production would be higher during hummingbird foraging periods than non-foraging periods. We measured nectar production in eight *B. costaricensis* plants during two time intervals: one hummingbird foraging period (morning) and one non-foraging period (midday). Contrary to our predictions, greater nectar production occurred at midday than during the morning. It may be that *B. costaricensis* are producing nectar when it is physiologically possible (during the warmest part of the day), independent of pollinator foraging behavior, or that pollinators of this plant forage in the evening more than in the morning or afternoon. We also found that *B. costaricensis* plants have highly skewed frequency distributions of nectar production across individual flowers (many flowers with little or no nectar and a few flowers with much nectar). This is consistent with a theory of a nectar allocation strategy in which plants benefit from providing occasional "bonanza" rewards for visitors.

Key Words: plant-hummingbird adaptations, pollination

Introduction

Many species of plants rely upon hummingbirds for pollination, and hummingbirds, in turn, rely on nectar for food. The temporal and spatial pattern of nectar production in some plants has co-evolved with the foraging patterns of the hummingbirds that pollinate them (Wolf 1976). For example, the bonanza theory (Feinsinger 1978) proposes that plants manipulate the spatial pattern of nectar production by producing little or no nectar in most flowers, with copious amounts in a few flowers. This strategy is thought to maximize hummingbird visitation per unit cost to the plant. Similarly, plants might regulate the production of nectar over time to maximize hummingbird visitation while minimizing energetic investment.

Bomarea costaricensis (Amaryllidaceae) occurs in the tropical highlands of Cerro de la Muerte, Costa Rica, and is visited by the volcano hummingbird *(Selasphorous flammula). S. flammula* is reported to forage most in the early morning (to compensate for loss of energy reserves overnight) and late afternoon (to accrue vital energy for the coming night; Chen et al. 1997). In some hummingbird-pollinated flowers, nectar production decreases after daybreak (Gill 1987), and ceases altogether by mid-morning (Feinsinger 1978), apparently to match the foraging patterns of their hummingbird pollinators. We hypothesized that *B. costaricensis* also varies its diel pattern of nectar production to match the foraging schedule of local hummingbirds.

Methods

On 29 January 2000, we examined diel variation in nectar production of *B. costaricensis* plants near the Cuerici Biological Station, Costa Rica. We selected eight inflorescences (containing at least 10 flowers of similar size), each on a separate *B. costaricensis* plant. After sundown on the day before data collection, we covered each flower cluster with cheese cloth to prevent nectar extraction by visitors. On the following day, we measured nectar production during two time intervals: one during the presumed hummingbird foraging period (0630 - 0830 h) and one during the presumed non-foraging period (1200 - 1400 h) (Chen et al. 1997). At the beginning and end of each time interval, we randomly collected two flowers per inflorescence, and measured the total volume of nectar per flower using 10 μL capillary tubes (volume = height of nectar in tube (mm) • 10 μL • 76.1 mm^{-1}). We also measured sugar concentration of nectar using an American Optical T/C hand refractometer. Pollinators were excluded with cheese cloth throughout the day.

To determine the mean nectar production during morning (foraging) and mid-day (non-foraging) periods for each inflorescence, we calculated the difference in mean nectar volumes per inflorescence from the beginning to the end of each interval. We tested effects of time interval and plant on nectar production (square-root transformed) with a two-way analysis of variance (SAS Institute 1997). The relationship between volume of nectar and sugar concentration was tested with a linear regression.

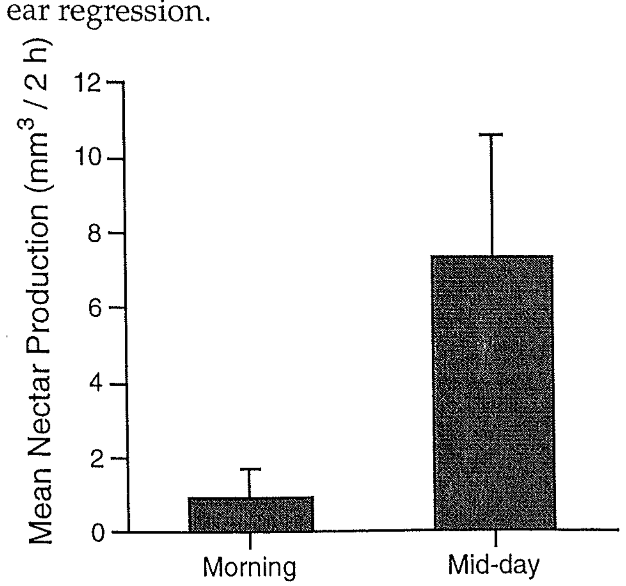

Figure 1. Mean nectar production (± SE) per flower in 8 *B. costaricensis* plants during two time intervals: morning (0630 - 0830 h) and mid-day (1200 - 1400 h).

Results

Nectar production was significantly greater during the mid-day interval than the morning interval (Fig. 1; $F_{1,7} = 5.53$, $p = 0.051$), and did not vary significantly between plants ($F_{7,7} = 1.71$, $p = 0.25$). The mean sugar concentration (± SD) was 25.0 ± 15.7 Brix degrees (n = 8), and sugar concentration appeared to be independent of nectar volume ($r = 0.17$, $p = 0.70$). However, because volumes ≥ 7 μL were required to measure sugar concentration, sample sizes for these measurements were limited and biased towards flowers with high nectar production. The distribution of nectar

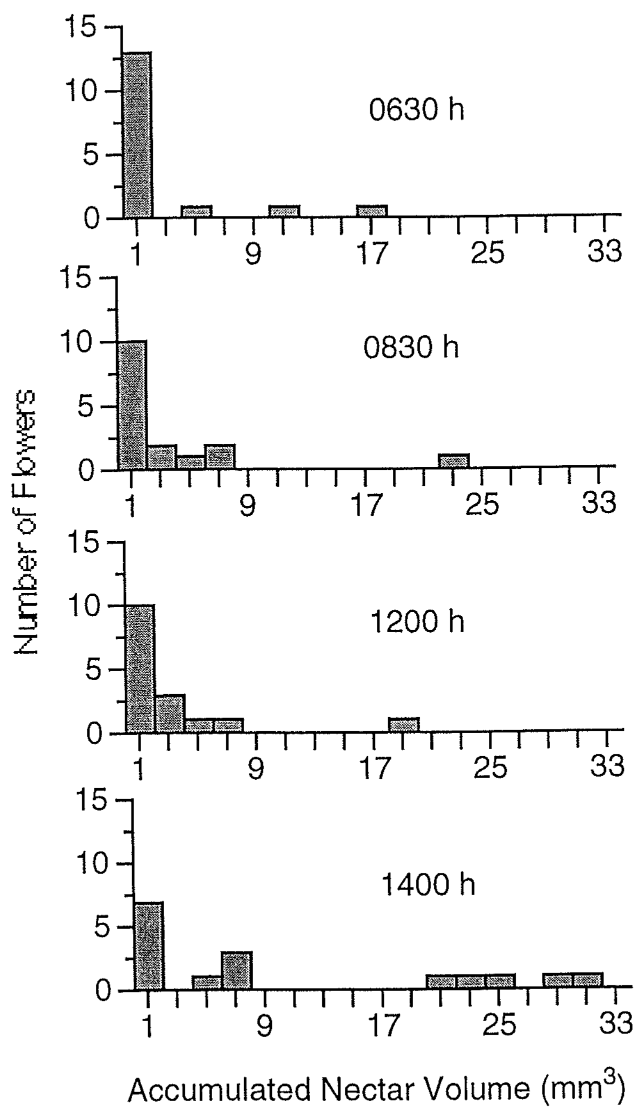

Figure 2. Frequency distribution of nectar volume in 16 flowers collected from 8 *B. costaricensis* inflorescences at four sampling times (0630, 0830, 1200, 1400 h). Nectar volumes were cumulative throughout the day.

between inflorescences was highly skewed during all four sampling times; a few flowers contained much nectar while most flowers contained none (Fig. 2).

Discussion

Contrary to our expectations, nectar production of *B. costaricensis* did not peak during the presumed morning hummingbird foraging interval. We offer three explanations for greater nectar production during the mid-day interval than the morning interval: physiological limitations of *B. costaricensis*, an inaccurate model of optimal timing of nectar production, or different foraging schedules of their hummingbird pollinators.

In the tropical highlands of Cerro de la Muerte, temperature varies greatly throughout the day, and high altitude plants may be limited to producing nectar only during the warmest part of the day. Therefore, *B. costaricensis* may not adjust its diel pattern of nectar production in relation to the foraging behavior of hummingbird pollinators, but simply produce nectar when conditions are optimal. Under this scenario, hummingbirds may be forced to adjust their foraging behavior to match the plant's schedule.

If *B. costaricensis* does adjust its pattern of nectar production in relation to the foraging behavior of hummingbirds, the observed timing of nectar production might be due to an inaccurate conception of optimal nectar production patterns. For example, it may be advantageous for *B. costaricensis* to produce most of its nectar in preparation for both morning and evening peak foraging periods, in which case our sampling only measured the afternoon pre-foraging build-up.

Alternatively, *B. costaricensis* could adjust its nectar production schedule according to pollinators that have different visitation patterns than the volcano hummingbird, which we used as our model simply because its diel behavior has been studied at Cuerici (Chen et al. 1997). Under this explanation, the flowers are producing nectar to match diel rhythms in their hummingbird pollinators, but the rhythms are different from those that we assumed. Further investigations of pollinator foraging schedules could test the relative importance of plant physiology vs. pollinator behavior patterns in the diel pattern of nectar production of *B. costaricensis*.

Our results revealed extensive variation in spatial distribution of nectar production among *B. costaricensis* flowers. Most flowers produced little or no nectar, while only a few produced large amounts. This pattern matches expectations of the bonanza theory of nectar rewards proposed by Feinsinger (1978). This, combined with the temporal patterns of nectar production, suggests that nectar production in *B. costaricensis* is optimized to maximize pollinator services relative to the expenses of nectar production. The consequences for hummingbirds of this spatial and temporal variation in nectar production are unclear. The temporal synchrony of nectar production and acquisition suggests a mutualistic relationship between the plant and its pollinator, but the bonanza pattern of variation among flowers suggests that the plant may be taking advantage of its hummingbird pollinators.

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